

Construction of a reference frame for studying changes in species composition in grasslands: the example of an old-field succession

Balent G.

in

Baudry J. (ed.), Bunce R.G.H. (ed.).
Land abandonment and its role in conservation

Zaragoza : CIHEAM

Options Méditerranéennes : Série A. Séminaires Méditerranéens; n. 15

1991

pages 73-81

Article available on line / Article disponible en ligne à l'adresse :

<http://om.ciheam.org/article.php?IDPDF=92605081>

To cite this article / Pour citer cet article

Balent G. **Construction of a reference frame for studying changes in species composition in grasslands: the example of an old-field succession**. In : Baudry J. (ed.), Bunce R.G.H. (ed.). *Land abandonment and its role in conservation*. Zaragoza : CIHEAM, 1991. p. 73-81 (Options Méditerranéennes : Série A. Séminaires Méditerranéens; n. 15)



<http://www.ciheam.org/>
<http://om.ciheam.org/>

Construction of a reference frame for studying changes in species composition in grasslands: the example of an old-field succession

GERARD BALENT

INSTITUT NATIONAL DE LA RECHERCHE AGRONOMIQUE
CENTRE DE TOULOUSE UNITE DE RECHERCHES SUR LES
SYSTEMES AGRAIRES ET LE DEVELOPPEMENT
BP 27 F-31326 CASTANET-TOLOSAN CEDEX
FRANCE

SUMMARY - Pyrenean grazing and crop land has been progressively abandoned to intensive production. This means that land is changed to grazing areas, grazing areas experience exportation of soil fertility, and abandonment of shepherding and herding allows animals to focus their consumption on the richer, greener areas. Under such conditions, the botanical composition of the land changes, going through a process of succession. Correspondence Analysis was used to determine the ecological patterns of vegetation in fields at different stages of abandonment. The model predicts the plant community dynamics and species turnover.

Key words: Correspondence Analysis, grazing, ecological succession, species diversity, community, sampling, Pyrenees.

RESUME - "Construction d'un cadre de référence pour l'étude des modifications de la composition des espèces dans les prairies: l'exemple de la succession dans les champs délaissés". Dans les Pyrénées, les pâturages et les terres cultivées ont été abandonnés peu à peu. Ceci signifie que les terres sont consacrées au pâturage, et qu'elles subissent une perte de fertilité du sol, et ainsi, le système pastoral étant abandonné, les animaux sont mis à pâturer dans des terrains bien plus riches et bien plus verts. Ces conditions font que la composition botanique des terres soit modifiée, un processus de succession ayant lieu. L'Analyse de Correspondances a été utilisée afin de déterminer la structure écologique de la végétation dans ces régions lors des différentes étapes de cet abandon. Le modèle utilisé prédit la dynamique de cette communauté végétale et de la succession des espèces.

Mots-clés: Analyse de Correspondances, pâturage, succession écologique, diversité des espèces, communauté, échantillonnage, Pyrénées.

Introduction

A community can be defined as a set of organisms from different species which coexist within the same habitat and interact across trophic and neighbourhood relationships (Lincoln *et al.*, 1982). Communities are generally open and overlap in a continuous way along environmental gradients rather than forming patches clearly separated (Whittaker, 1967; Giller, 1984). Studies on relationships between species composition of communities and their habitat are numerous, either to compare the difference in species composition between different habitats, or to analyze the evolution of species composition in time (Whittaker, 1967; 1973; Austin, 1980; Austin and Austin, 1980; Naveh and Whittaker, 1980; Housard *et al.*, 1980; Bouxin and Gautier, 1982; Hutchings, 1983; Willens, 1983; Balent and Duru, 1984; Van der Maarel, 1988) stressed the importance of gradient analysis and ordination to answer these questions.

Methodological problems are inherent to these approaches. Some authors focus on relevés ordination, others on species ordination, a few on both species and relevés ordination (Prodon and Lebreton, 1981). Moreover there are many questions about choice and validity of ordination methods with an "over-emphasis on methodology and technique rather than ecological application, low levels of use in applied studies and an increased tendency to use complementary and multiple analysis" (Kent and Ballard, 1988).

In this paper, I want to illustrate the capacities of Correspondence Analysis (CA) to answer with both mathematical and ecological accuracy two questions related to vegetation dynamics. What are the main ecological factors gradually affecting the structure and evolution of species composition of communities? These gradients can be defined either a priori and then, we have to fit the species composition to them, or a posteriori from the changes in species composition (i.e. like factorial

axes are), and then we have to determine the significance of these gradients from correlation with extra data on environment (Prodon and Lebreton, 1981; Hacker, 1983). What is the value of the ordination of species along a defined a posteriori environmental gradient? The accuracy of the answer of the different species mainly depends on the quality of the sampled ecological universe (Balent and Courtiade, 1990). If a type of environmental condition is overlooked, the relative answer of the species differs.

The comparison of a set of relevés with CA allows us to establish a hierarchy of independent ecological factors acting on the structure and dynamics of the communities (Lacoste and Roux, 1971; 1972; Guinochet, 1973; Montard and Gachon, 1978; for plant community). For a given species x relevés matrix, CA extracts the maximum of variance from the matrix (Lebreton *et al.*, 1988) and provides the best reciprocal ordination of the species and the relevés (Benzecri *et al.*, 1973; Esteve, 1978; Chessel *et al.*, 1982). It is a useful tool to model the turn-over of species along the different ecological factors or gradients (Prodon and Lebreton, 1981) and provides new measurements of Habitat Amplitude (HA) and Ecological Diversity (ED) of the relevés along these gradients (Chessel *et al.*, 1982; Prodon, 1988).

In this paper, I give an example of the possibilities of Correspondence Analysis analyzing an old-field succession in the French Pyrenees.

Rationale and methods

1. The old-field succession

For reasons which we will not go into here, the Central Pyrenees suffered, between 1850 and 1900, a loss of 40% of its population. Pressure on the land diminished at the same time as available labour declined. Crop-fields started diminishing at the beginning of the century and were replaced by hay-fields. The hay-fields started disappearing significantly after the nineteen fifties under the effects of the development of mechanical farming and the drop in the number of animals. In the ô valley, where this work was conducted, cultivated land dropped from 100 to 10 ha, while hay-fields declined from 100 to 75 ha. Thus a total of more than a hundred hectares have become grazing land used in a collective way in association with communal lands.

These areas (commons, old meadows, old fields) are now not fertilized at all. Animals eat the grass and export the greatest part of the fertilizing elements; they only return a small fraction with their droppings, they leave manure in the buildings which is then only spread on the crop-fields and the hay-fields (Balent and Duru, 1984). When a crop-field is transformed into a hay-field, its annual productivity of dry matter is very high

at the beginning, due to the large reserves of fertilizer elements left from manure farming practices. It then drops exponentially during twenty to twenty-five years until it stabilizes at a level corresponding to the amount of manure spread. So whatever the land use is, the fertility of the fields always decreases along the old-field succession.

The abandoning of herding obligations in the valley bottom areas soon followed by the disappearance of the permanent communal shepherds and cowherds, is the second decisive evolution in grazing practices. Free ranging animals are attracted to those parts of the land with the best flora and the greenest grass (Arnold and Dudzinski, 1978; Low *et al.*, 1981; Balent, 1987) and most often go to the most fertile and best maintained areas (hay-fields and old-fields). In leaving the marginal areas which have long since not been cultivated or cut, they accelerate the process of land returning to the wild.

2. Sampling design

Seventy fields were selected by a stratified sampling of the diversity of the pastoral territory of the valley according to the range of variation of two a priori important factors: the management history (Balent and Duru, 1984) and the actual grazing pressure estimated from observations on the grazing and spatial behaviour of grazing cattle and sheep (Balent, 1987). Botanical composition is measured with the quadrat-point method (50 points along a 20 m line)

3. Data processing

3.1. Modelling the old-field succession

The 70 relevés x 223 species matrix was analyzed by Correspondence Analysis (CA) (Benzecri *et al.*, 1973). Recently, several papers have tried to compare and discuss the set of classification and ordination methods in plant ecology (Minchin, 1987; Kent and Ballard, 1988; Knox, 1989). Gauch (1982) severely criticised CA specially because of the distortion caused by the Guttman effect (arch shoe effect) at the poles of the F1 axis. To correct the arch-shoe effect Gauch in 1982 proposes to artificially equalize the variance along the factorial axes and so changing the scores of the species and the relevés. Consequently, Detrended Correspondence Analysis loses probably the most interesting property of CA for purpose of ordination: the canonical correlation obtained between species and relevés (Benzecri *et al.*, 1973; Esteve, 1978; Chessel *et al.*, 1982). Another criticism of Gauch is on the non-independence of the first and second axes of CA. As it is shown here after a mathematical artifact does not imply automatically an ecological artifact.

I run CA on cover data prior to presence data because "transformation of vegetation cover data to presence data ignores the details of the local species dynamics and emphasizes the coarser grained signal of local species extinction and colonization" (Allen and Wyleto, 1983; Allen, 1987). Presence data are to be used when the main focus of the study is on the relationships between plants and physical environment i.e. on the upper levels of plant distribution. Otherwise, vegetation cover data are more suitable to study local evolution i.e. community dynamics at lower levels of organization where the abundance of species evolves more rapidly than botanical composition. Plantureux *et al.*, (1987) have nicely illustrated this point for intensively managed grasslands.

3.2. Habitat Amplitude (HA) and Ecological Diversity (ED)

Chessel *et al.*, (1982) have proposed a definition for Habitat Amplitude (HA) and Ecological Diversity (ED) based on the reciprocal ordination of species and relevés provided by CA.

Habitat Amplitude (HA) of a species is defined by the more or less important dispersion of the relevés where the species is present along an ecological gradient.

In the same way, for a given set of species ranked along a gradient, the dispersion of all the species of one relevé along this gradient can be considered as a measurement of the ecological diversity of the relevé (Chessel *et al.*, 1982). This ecological diversity increases with the dispersion of the species of the relevé on the gradient. It does not depend upon the number of species as the Shannon Index does, but simply on the ecological response of the different species along the gradient. As a diversity measurement, ED gives an optimal account of the within-relevés diversity (α -diversity) (Chessel *et al.*, 1982).

Results and discussion

Ecological factors influencing botanical composition

From the scores of both species and relevés and extra information on past and present management of the fields, we have established (Balent and Duru, 1984; Balent, 1986, 1987) that F1 ordination (canonical correlation= 0.66) was a residual fertility gradient and F2 (canonical correlation= 0.50) a grazing pressure gradient reflecting the present management of the plant communities. The significance of these two factors reflects of course the sampling methods. Here the main purpose is

ordination of species and relevés according to ecological factors which importance was established *a priori*.

The two highly significant relationships demonstrate that, despite the arch-shoe effect, axes F1 and F2 reflect an ecological reality.

$$F1=A+B(IP)+C(IK) \quad n=18 \quad R^2=.87^{***}$$

PI and KI are respectively indices of phosphorus and potassium uptake by plants (Balent and Duru, unpublished data);

$$F2=A'+B'(DM) \quad n=23 \quad R^2=.51^{***}$$

DM = Dry Matter collected by grazing animals (Balent, 1987).

The present management practices (F2) are a function of the residual fertility (F1) as it was shown by Balent and Duru, 1984; Balent, 1987). Esteve (1978) highlighted the point that the mathematical independence of the successive axes carried out by CA did not imply their ecological independence.

Modelling the plant community dynamics

The interaction between F1 and F2 models the relationships between the past and present management of the valley's pastoral territory (Fig. 1). Indeed all of the fields, representing the total valley bottom land area, are to be found between two "envelop" curves (a) and (b). The few fields located to the left of the curve (a) correspond to the transition between herbaceous vegetation types and overgrown abandoned fields. The (b) curve represents the maximum value observed in the present management system, of the grazing pressure as a function of the residual fertility of soils.

At first, if it has not been grazed, which is rather rare because of common winter grazing, it will quickly become overgrown abandoned land (T1 trajectory). Otherwise, the animals through their trampling will contribute to the gradual disappearance of wild species (e.g. *Urtica* sp., *Arctium minus*) and will favour the growth of good grazing species (e.g. *Dactylis glomerata*, *Trifolium repens*, *Poa pratensis*). The appetibility of the vegetation and the pastoral value will increase, and given the absence of shepherding, so will visits by the animals. The flora will continue to improve and the pastoral value of the field will reach its maximum at the same time as the frequency of animal visits.

Secondly, the continuous decrease of soil fertility because of leaching and grazing exportation of the fertilizing elements, will lead to the disappearance of the most demanding vegetation species and consequently to the diminishing of the pastoral value. The animals will then abandon it to visit fields which have not been

abandoned so long and which in their turn, have reached their maximum pastoral value. This scenario, which is the most widespread, corresponds to T3 or T4 type evolution trajectories according to the intensity of the grazing pressure following abandonment of cultivation. The fields end up by either stabilizing with a lawn type vegetation, or by evolving towards a coppice type (T2) vegetation if they are located near a hedge or a wood.

This model can be used to characterize the different evolutionary modes for pastoral areas. It can also be used to estimate the speed of these evolutions. Using surveys of retired farmers, and studies of aerial photography, we estimated that the evolutionary speed of an abandoned field roughly follows a logarithmic scale along F1. This hypothesis as well as the validity of the evolutionary trajectories for the fields have been confirmed by the shifting of fields introduced into the model after 5 years of evolution (Fig. 1: Balent, 1987).

Modelling the species turn-over along the old-field succession

1. Ecological Diversity

The main goal of diversity measurement within a community is to give an account of its degree of organization. (Goodman, 1975). Within a region, the nature of community diversity is double and depend upon the diversity between relevés (β -diversity) and within relevés (α -diversity) (Whittaker, 1972; Routledge, 1984). CA maximizes β -diversity and minimizes at the same time α -diversity (Prodon, 1988).

A lot of indices have been used to characterize the degree of organization of a community. To illustrate the basic difference between structural and functional indices I present on Figs. 2 and 3 the behaviour, along F1 and F2 axes of CA, of Species Richness, Shannon H' Index and Ecological Diversity *sensu* Chessel *et al.*, (1982).

Species richness and H' present the same patterns of variation along F1. The general trend is toward an increase with the age of the community even within group of fields with heavy grazing. The ecological diversity (F1- diversity) behaves in an opposite way decreasing with time. In fact, the F1-diversity presents strong values at the early stages of the succession that drops to a more or less constant value till the end of succession.

As I mentioned above, the ecological diversity increases with the dispersal of the species of the relevés along the factorial axis. In the early stages of old-field succession, the plant density is low and the high residual fertility prevents a high competition level, so species with different ecological preferences may coexist within the same old-field.

Competition increases with grazing pressure (Donald, 1963) and with the loss of fertility. New species invade the field but only species well fitted to local condition of grazing pressure and residual fertility. The stabilization of F1-diversity at a low level reflects the ecological coherence of the community: all the species have similar ecological preference along F1, and the mean ecological response of the community and of the species are the same. In the following stages of the succession, F1-diversity is constant while the number of species increases. This probably means that, in the relevés corresponding to the last stages of the old-field succession, the species should have very close ecological preferences.

Along the F2 gradient of grazing pressure, species richness and Shannon diversity behave in the same way, minimum values are at the extremes of the axis and maximum values for intermediate grazing pressure. This pattern seems to be classical (Collins and Barber, 1985) even if different results have been established (Macnaughton, 1983). In fact, if we except the early stages of the old-field succession where grazing pressure constrained the structure of the community, species richness and Shannon diversity decrease when grazing pressure increases.

Ecological diversity (F2-diversity) roughly behaves along F2 as it does along F1. Early stages of old-field succession present a high F2-diversity for the reasons I gave above i.e. mainly a poor competitive environment. Otherwise the F2-diversity remains constant along a wide range of grazing pressure. Grazing pressure acts on the ecological coherence of the community along F2 like residual fertility on F1 does. The main difference is in the decreasing number of species while grazing pressure increases i.e. a diminishing number of species occupied the same ecological space. But when grazing pressure reaches the highest levels F2-diversity starts increasing again. Animal treading creates patches of bare ground invaded by propagules of species necessarily not well adapted to heavy grazing pressure. Overgrazing can then be defined as the grazing pressure level when the ecological coherence of the community is changed.

2. Habitat Amplitude

The measurement of HA proposed by Chessel *et al.*, (1982) presents, compared to very close techniques (Daget and Godron, 1982), some decisive advantages such as the canonical correlation of the reciprocal ordination of species along ecological gradients defined *a posteriori* (indirect gradient analysis).

HA provides a measurement of the ecological amplitude of a species within a community along one niche

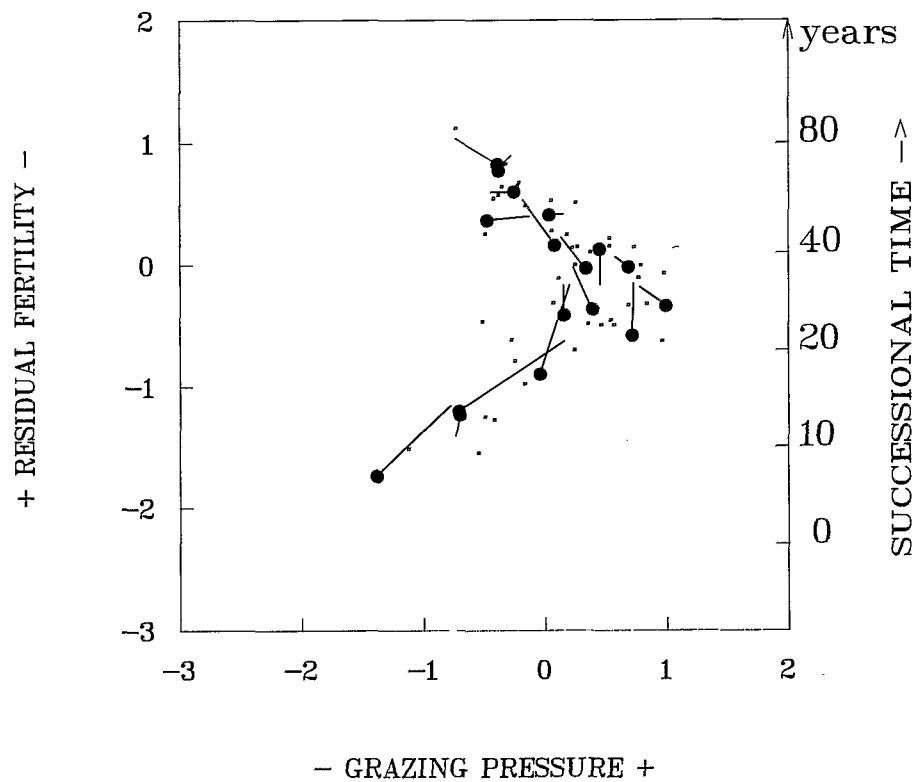
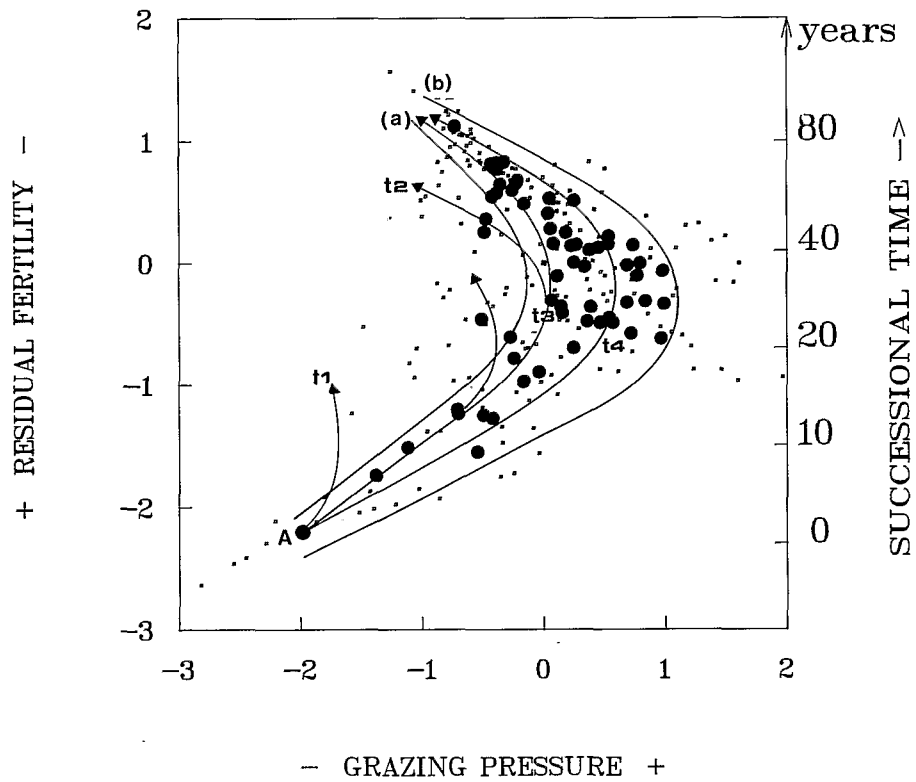


Fig. 1. Trajectories of evolution of grassland communities in the Pyrenees after the abandonment of cultivation on the factorial plan (F1,F2).
 (up: Theoretical trajectories; down: Observed trajectories over 5 years)

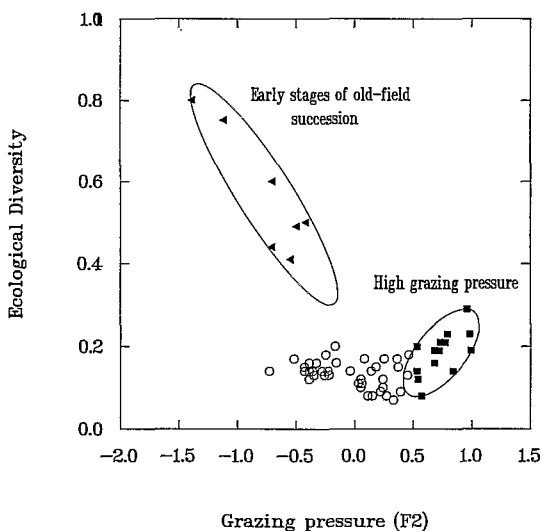
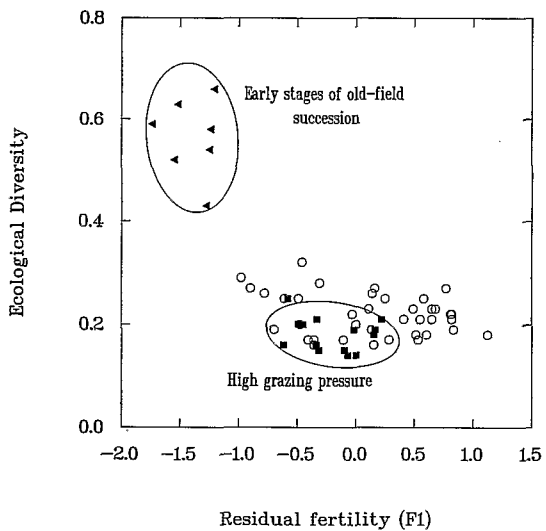
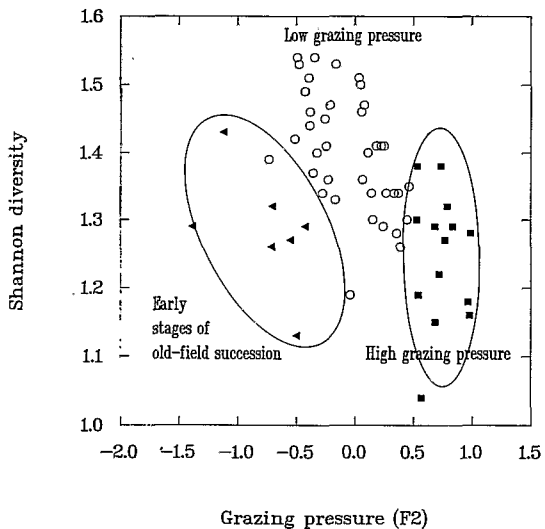
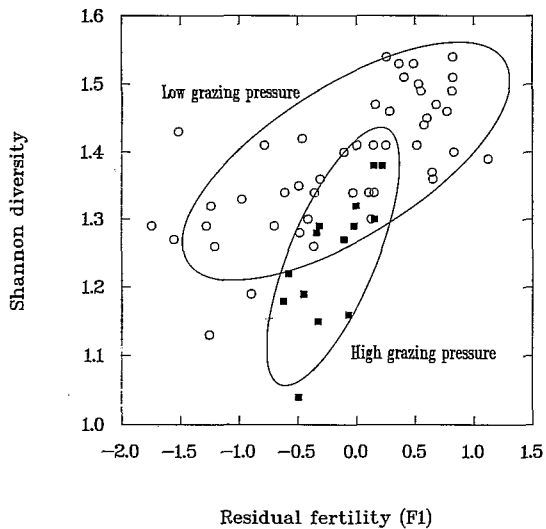
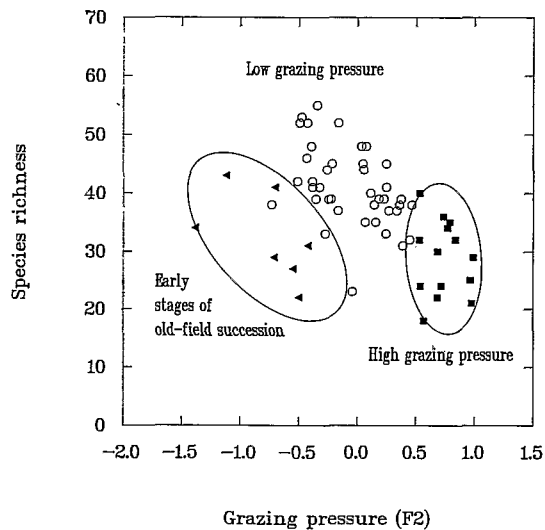
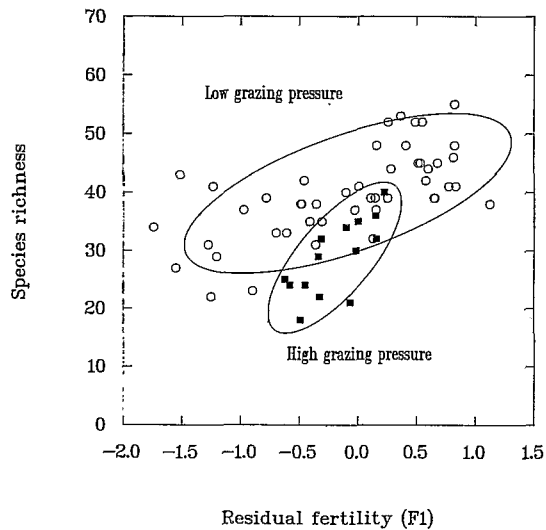


Fig. 2. Patterns of variation along F1 axis (residual fertility) of some structural and functional indices of diversity.

Fig. 3. Patterns of variation along F2 axis (grazing pressure) of some structural and functional indices of diversity.

dimension. This dimension is not a resource as in the Hutchinson hyper-volume (Hutchinson, 1958) but an ecological factor constraining the structure of the community.

Fig. 4 shows the variation of Habitat Amplitude along F1 and F2 axes and the ecological preferences of the species (scores on the axes). HA exhibits a classical pattern of variation: minimal values are at the extremes

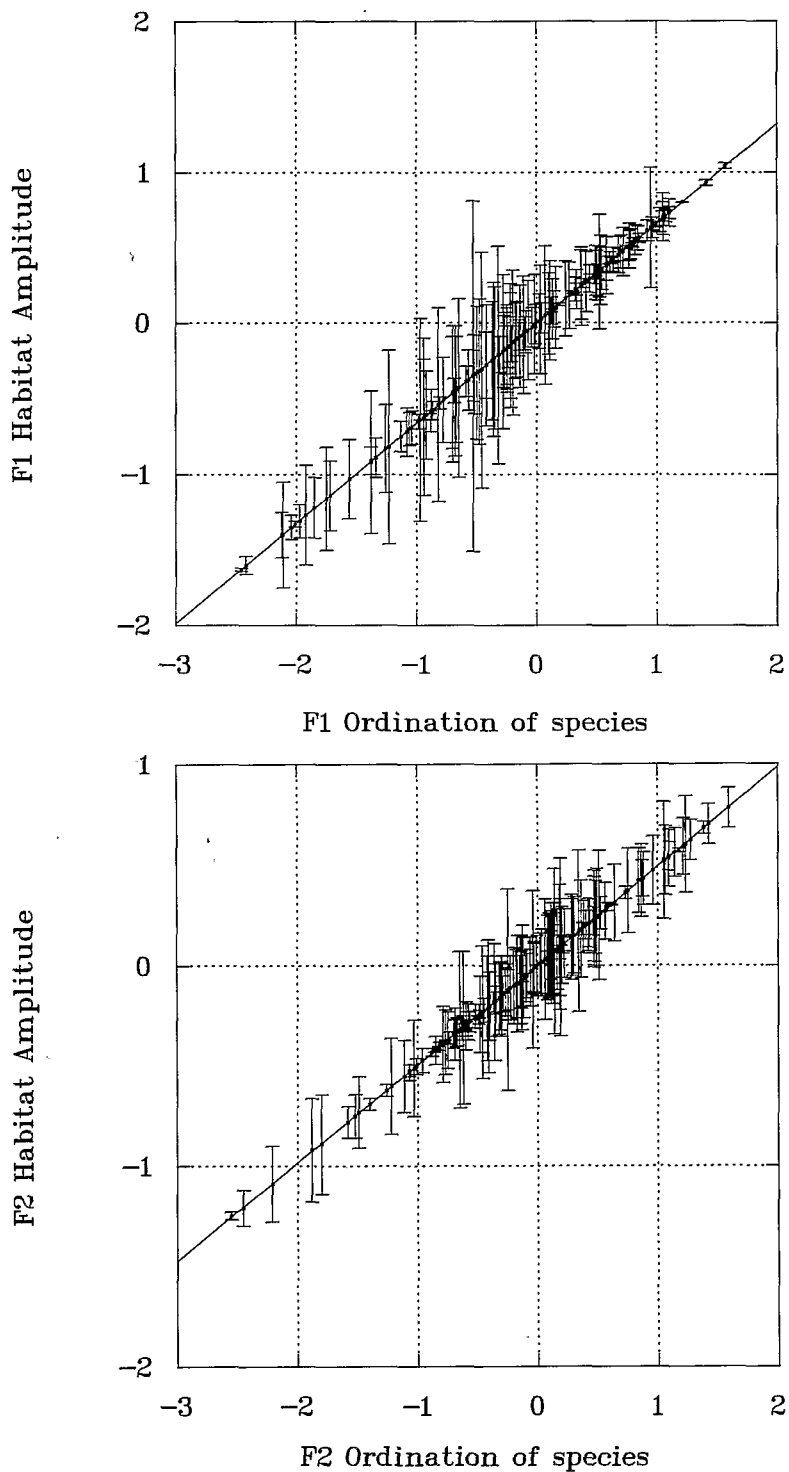


Fig. 4. Patterns of variation of Habitat Amplitude of 223 species along the F1 axis (upper part) and the F2 axis (lower part). The vertical bars represent, for each species, the variance of its distribution along the factor.

of the axes and maximal values at the intermediate axes. This simply means that specialist species are only found at the beginning and at the end of the two gradients.

A wide HA may be the result of the coexistence, within the same community, of phenotypes differing in their ecological preferences, or of a single generalist one. A narrow HA helps us to define a set of species with good indicator values for applied ecological purpose.

Conclusion

As shown in this example of old-field succession, Correspondence Analysis constitutes a useful tool to build a model of changes in species composition of communities. But I want to outline the importance of sampling design. The choice of the sites has to be considered as a real experimental design in order to avoid missing some existing state of the studied ecological system. By introducing or eliminating relevés in CA in the first steps of the analysis, we can maximize the canonical correlation of the reciprocal ordination between species and relevés and thus improve the quality of the measurement of the ecological preferences of the species within the community. The consequence is in a better expression of the Habitat Amplitude which enable us to measure the turn-over of species along the gradients and of the Ecological Diversity.

Measurement of ED is probably the most significant advantage of CA. As it has been shown above, this index is not a simple measurement index of the structural diversity of the community like a lot of diversity measurement indices are, it is a functional index giving account of the ecological coherence of the community. Traditional diversity indices are based on relative abundance of the species and overlook the ecological characteristics of species. On the other hand, the index proposed by Chessel *et al.*, (1982) constitutes a diversity index *sensu stricto* (diversus = opposite, Prodon pers. comm.) as based on the ecological answer of the species. Thus it provides informations not only on the degree of ecological homogeneity/heterogeneity of the species composition but also, in our example of the Pyrenean grasslands, on the stability/ instability of the species assemblage.

Effectively, the constancy of the value of the F1 and F2 diversities along the respective axes is a result of the slowness of the evolution of the botanical composition of the community after the abandonment of cultivation. The turn-over of species has been so slow that at any stage of the succession (except the early stages for F1 and F2 and overgrazing for F2) both the ecological answer of one relevé and of the species it owned are the same.

The possibility to introduce extra relevés into the model allows us to analyse the changes occurring in species composition of communities in a diachronic way by introducing the same site at different dates (see the validation of the trajectories of evolution), or a synchronic way by introducing sites of different ages.

For example, if we introduce in the model a data set from other regions where agricultural practises are different, the ecological diversity behave differently compared to the Pyrenees (Balent, in prep.). High levels of disturbance e.g. over 300kg/ha/year of mineral Nitrogen, lead the ecological diversity to fall to a very low level, only a few ecologically similar species being able to stand so intensive management. On the contrary, a sudden reclamation of a very old oligotrophic community lead ED to increase because species of rich environment invade the site. So ED constitute a very promising tool to investigate community structure and evolution from a theoretical and a practical point of view.

Acknowledgements

This work is supported by the Agrarian System Department of INRA and by a special grant of the Ministry of Environment of France (EGPN Committee) to study "The ecological consequences of agriculture abandonment".

References

- ALLEN, T.F.H. (1987): Hierarchical complexity in ecology: a noneuclidean conception of the data space. *Vegetatio*, 69: 17-25.
- ALLEN, T.F.H. and WYLETTO, E.P. (1983): A hierarchical model for the complexity of plant communities. *Journal of Theoretical Biology*, 101: 529-540.
- ARNOLD, G.W. and DUDZINSKI, M.L. (1978): Developments in animal and veterinary sciences. 2: Ethology of free ranging domestic animals. Elsevier, Amsterdam, 198 pp.
- AUSTIN, M.P. (1980): An exploratory analysis of grassland dynamics: an example of a lawn succession. *Vegetatio*, 43: 87-94.
- AUSTIN, M.P. and AUSTIN, B.O. (1980): Behaviour of experimental plant communities along a nutrient gradient. *Journal of Ecology*, 68: 891-918.
- BALENT, G. (1986): The influence of grazing on the evolution of botanical composition of previously cultivated fields. The example of the Pyrenees. Pages 28-29 *in*: Rangeland: a resource under siege (Joss, P.J., Lynch, P.W. and Williams, O.B., eds.). Australian Academy of Science, Canberra.
- BALENT, G. (1987): Structure, fonctionnement et évolution d'un système pastoral. Le pâturage vu comme un facteur écologique piloté dans les Pyrénées centrales. Thèse de Doctorat d'Etat, Université de Rennes 1, 146 pages + annexes.

- BALENT, G. and DURU, M. (1984): Influence des modes d'exploitation sur les caractéristiques et l'évolution des surfaces pastorales: cas des Pyrénées centrales. *Agronomie*, 4 (2): 113-124.
- BALENT, G. and COURTIADÉ, B. (1990): Modelling landscape changes in a rural area of South-Western France. *Landscape Ecology*, (submitted)
- COLLINS, S.L. and BARBER, S.C. (1985): Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio*, 64: 87-94.
- BENZECRI, J.P. et coll. (1973): L'analyse des données. II. L'analyse des Correspondances. Dunod, Paris, 619 pp.
- BOUXIN, G. and GAUTIER, N. (1982): Pattern analysis in Belgium limestone grasslands. *Vegetatio*, 49: 65-83.
- CHESSSEL, D., LEBRETON, J.D. and PRODON, R. (1982): Mesures symétriques d'amplitude d'habitat et de diversité intra-échantillon dans un tableau espèces-relevés: Cas d'un gradient simple. C.R. Académie des Sciences de Paris, T. 295, Série 3, 83-88.
- DAGET, PH. and GODRON, M. (1982): Analyse fréquentielle de l'écologie des espèces dans les communautés. Masson, Paris, 163 pp.
- DONALD, C.M. (1963): *Competition among crops and pasture plants*. Advance in Agronomy, 15: 1-118.
- ESTEVE, J. (1978): Les méthodes d'ordination: éléments pour une discussion. Pages 223-250 in: *Ecologie et Biométrie* (Legay, J.M. and Tomassone, R., eds.). Société Française de Biométrie, Paris.
- GAUCH, H.G. (1982): *Multivariate analysis in community ecology*. Cambridge Studies in Ecology. Cambridge University Press, Cambridge, UK.
- GILLER, P.S. (1984): *Community structure and the niche*. Chapman and Hall, London, UK.
- GOODMAN, D. (1975): The theory of diversity-stability relationships in Ecology. *The Quarterly Review of Biology* 50 (3): 237-266.
- GUINOCHET, R. (1973): *La phytosociologie*. Masson, Paris.
- HACKER, R.B. (1983): Use of reciprocal averaging ordination for the study of range condition gradients. *Journal of Range Management* 36: 25-30.
- HOUSSARD, C., ESCARRE, J. and ROMANE, F. (1980): Development of species diversity in some Mediterranean plant communities. *Vegetatio* 43: 59-72.
- HUTCHINGS, M.J. (1983): Plant diversity in four chalk grassland sites with different aspects. *Vegetatio* 53: 179-189.
- HUTCHINGSON, G.E. (1958): Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22: 415-427.
- KENT, M. and BALLARD, J. (1989): Trends and problems in the application of classification and ordination methods in plant ecology. *Vegetatio*, 109-124.
- KNOX, R.G. (1989): Effects of detrending and rescaling on correspondence analysis: solution stability and accuracy. *Vegetatio* 83: 129-136.
- LACOSTE, A. and ROUX, M. (1971): L'analyse multidimensionnelle en phytosociologie et en écologie. 1: L'analyse des données floristiques. *Oecologia plantarum* 6: 353-369.
- LACOSTE, A. and ROUX, M. (1972): L'analyse multidimensionnelle en phytosociologie et en écologie. 2: L'analyse des données écologiques et l'analyse globale. *Oecologia plantarum* 7: 125-146.
- LEBRETON, J.D., CHESSSEL, D., PRODON, R. and YOCOZ, N. (1988): Analyse des relations espèces-milieu par l'Analyse Canonique des Correspondances. 1. Variables de milieu qualitatives. *Acta Oecologica/ Oecol. Gener.* 9: 53-67.
- LINCOLN, R.J., BOXSHALL, G.A. and CLARK, P.F. (1982): *A dictionary of ecology, evolution and systematics*. Cambridge University Press, Cambridge, UK.
- LOW, W.A., DUDZINSKI, M.L. and MULLER, W.J. (1981): The influence of forage and climatic conditions on range community preference of shorthorn cattle in central Australia. *Journal of Applied Ecology* 18: 11-26.
- MACNAUGHTON, S.J. (1983): Serengeti grassland ecology: The role of composite environmental factors and contingency in community organization. *Ecological Monographs* 53 (3): 291-320.
- MINCHIN, P.R. (1987): An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69: 89- 108.
- MONTARD, F.X. DE and GACHON, L. (1978): Contribution à l'étude de l'écologie et de la productivité des pâturages d'altitude des Monts Dore. I. Application de l'analyse factorielle des correspondances à l'analyse de la végétation. *Annales Agronomiques*, 29 (3): 277-310.
- NAVEH, Z. and WHITTAKER, R.H. (1980): Structural and floristic diversity of shrublands and woodlands in Northern Israel and other mediterranean areas. *Vegetatio* 41: 171-190.
- PLANTUREUX, S., BONISCHOT, R. and GUCKERT, A. (1987): Effet des techniques d'intensification sur l'évolution de la végétation de prairies permanentes lorraines. *Acta Oecologica/Oecol. Appli.* 8: 229-246.
- PRODON, R. (1988): Dynamique des systèmes avifaune-végétation après déprise rurale et incendies dans les Pyrénées Méditerranéennes Siliceuses. Thèse Doctorat d'Etat, Univ. P. and M. Curie, Paris VI: 333 pp.
- PRODON, R. and LEBRETON, J.D. (1981): Breeding avifaune of a mediterranean succession: the Holm oak and cork oak series in the eastern Pyrenees. I, Analysis and modelling of the structure gradient. *Oikos* 37: 21-38.
- ROUTLEDGE, R.D. (1984): Estimating ecological components of diversity. *Oikos* 42: 23-29.
- VAN DER MAAREL, E. (1988): Species diversity in plant communities in relation to structure and dynamics. Pages 1-14 in: *Diversity and patterns in plant communities* (During, H.J., Werger, M.J.A. and Willems, J.H., eds.). SPB Academic Publishing, The Hague, The Netherlands.
- WILLEMS, J.H. (1983): Species composition and above-ground phytomass in chalk grassland with different management. *Vegetatio* 52: 171- 180.
- WHITTAKER, R.H. (1967): Gradient analysis of vegetation. *Biological Review* 42: 207-264.
- WHITTAKER, R.H. (1972): Evolution and measurement of species diversity. *Taxon* 21: 213-251.
- WHITTAKER, R.H. (1973): Direct gradient analysis: Techniques and results. Pages 7-52 in: *Ordination and classification of communities* (Whittaker, R.H., ed.). Junk, The Hague.